Low-temperature incubation of walleye pollock (*Theragra chalcogramma*) eggs from the Southeast Bering Sea shelf and Shelikof Strait, Gulf of Alaska

by

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Abstract

To determine the effect of low water temperature on development, walleye pollock (*Theragra chalcogramma*) eggs from the Bering Sea were reared at -0.6°, 0.4°, 2.0°, and 3.8°C. One group of eggs was reared at 3.9°C under a diel light cycle (14 h light, 10 h dark) to observe the effect of light on development and hatching. Development was normal for all temperatures except -0.6°C; abnormal development of the tail and lack of development of eyes occurred in some embryos. Time to 50% hatch was 820, 620, and 424 h at 0.4°, 2.0°, and 3.8°C. Eggs incubated in diel light at 3.9°C developed at the same rate as eggs incubated in constant dark at 3.8°C, but required an additional 72 h to reach 50% hatch. A piece-wise regression model was generated to predict egg age for incubation temperatures of -0.6 - 3.8°C. For temperatures recorded in the southeastern Bering Sea 1995-1998, the model predicted incubation periods for walleye pollock eggs that varied by 13 days between the warmest and coldest years.

Walleye pollock eggs from Shelikof Strait, Alaska, were incubated at 0.2°, 1.8°, and 2.8°C. Development was normal for all temperatures. A piece-wise regression model (as above) was generated for incubation temperatures 0.2 - 2.8°C. When the regression models were compared, Bering Sea eggs (1.4-1.7 mm in diameter), required more time for development prior to hatch than Shelikof Strait eggs (1.2-1.3 mm in diameter) at 1.8° and 2.8°C. However, for temperatures 0.2-2.0°C, Bering Sea walleye pollock began hatching earlier and at a developmentally younger age than Shelikof Strait walleye pollock.

Keywords: *Theragra chalcogramma*, walleye pollock, fish eggs, incubation, low temperature
Regional index terms: Bering Sea; Gulf of Alaska, Shelikof Strait

Introduction

Development rates for fertilized eggs of walleye pollock (*Theragra chalcogramma*) are required for many analyses of their early life history. These development rates vary with temperature and between different populations (Blood *et al*., 1994). This paper estimates low-temperature (-0.6 - 3.8°C) development rates for walleye pollock eggs that were spawned from the southeastern Bering Sea and Shelikof Strait, Alaska. Prior to this study, egg development rates were not available for the Bering Sea population.

Egg development rates are well documented for other populations of walleye pollock in Japan and the Gulf of Alaska (Hamai *et al*., 1971; Haynes and Ignell, 1983; Nakatani and Maeda, 1984; Blood *et al*., 1994) and have been used to estimate early life-history parameters of walleye pollock such as abundance and distribution of eggs by age intervals (Kendall and Kim, 1989: Kendall and Picquelle, 1990; Kendall *et al*., 1994), and egg production and mortality (Picquelle and Megrey, 1993; Brodeur *et al*., 1996). These parameters play an integral part in individual-based modeling (IBM) of egg, larval, and juvenile stages (Hinckley *et al*., 1997) which, in turn, has been combined with a circulation model to form a coupled biophysical model that produces spatial distributions of the early life stages of walleye pollock in Shelikof Strait, Alaska (Hermann *et al*., 1996). Existing models of temperature-specific development rates of walleye pollock eggs are inappropriate to use for IBM and biophysical models of the southeastern Bering Sea because they are based on populations that are too distant from the Bering Sea (Hamai *et al*., 1971; Nakatani and Maeda, 1984) or on incubation temperatures that are too warm (Haynes and Ignell, 1983; Blood *et al*., 1994). The walleye pollock egg production model developed for Shelikof Strait, Alaska (Picquelle and Megrey, 1993) is based on incubation temperatures between 3.8° and 7.7°C (Blood *et al*., 1994) and is not valid at temperatures outside that range. In 1995, temperatures between -1.5° and 2°C were recorded within southeastern Bering Sea shelf walleye pollock nursery areas (Stabeno *et al*., 1998). Other walleye pollock egg development models encompass these low temperatures (Nakatani and Maeda, 1984; Haynes and Ignell, 1993), but they are based on fish populations in Funka Bay, Japan, and near Juneau, Alaska,

whose eggs incubate in water that is typically warmer (2-6°C and 4-10°C, respectively) (Kendall and Nakatani, 1992; Coyle and Shirley, 1990) than the low temperatures recorded in the southeastern Bering Sea shelf region.

Nakatani and Maeda (1984) reported malformations of embryos incubated at -1°C; it is not known whether those malformations were the result of that particular sample of eggs being exposed to such a low temperature, or if eggs of all stocks of walleye pollock would exhibit similar aberrant development. Data collected in 1995 and in more recent years documenting low temperatures (<1°C) throughout the water column (Stabeno *et al*., 1998; Stabeno *et al.*, this volume), and the periodic extension of the subsurface cold pool (Wyllie-Echeverria and Ohtani, 1999) into areas in which walleye pollock eggs have been collected demonstrate that, although walleye pollock may prefer not to spawn in cold water areas (i.e., <2°C), their eggs may be advected into these areas. For example, eggs approximately 24 h old were collected near the 2°C boundary near Unimak Island, Alaska on 23 April 1995 in water that was <2°C [1]; it is not known whether the water was <2°C at the time the eggs were spawned or if it cooled soon after. The impact of the cold water on incubation time of the eggs and possible developmental abnormalities are best assessed with eggs from fish whose population has frequently been exposed to these low temperatures (Blood *et al*., 1994).

In addition, none of the existing models address the effect of light on length of incubation. Olla and Davis (1993) demonstrated that walleye pollock eggs incubated under diel light conditions experienced a delay in hatching rate compared to eggs incubated in constant dark. However, this work was on Shelikof Strait walleye pollock eggs that are found 150-200 m deep and are not normally exposed to levels of light typical of the upper water column. Exposure to light may have a different effect on such eggs than on those from the southeastern shelf region of the Bering Sea, much of which is <100 m in depth, where walleye pollock eggs

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can be distributed in great numbers in the upper 25 m of the water column (Waldron and Vinter, 1978; Nishiyama *et al.*, 1986; Kendall, 2001). The effect of light on the length of incubation should be tested on eggs that are typically distributed throughout the upper water layer.

A model of temperature-specific development rates based on Southeast Bering Sea walleye pollock eggs at temperatures occurring in that region, and the influence of light on hatching rates, when used in conjunction with previous data from the Shelikof Strait, would expand the range of temperatures over which development rates can be modeled. This would, in turn, greatly enhance southeastern Bering Sea shelf walleye pollock egg and larval vertical distribution research and IBM and biophysical models of the Bering Sea ecosystem. However, prior to combining cold-water incubation data on Bering Sea eggs with warmer-water data on Shelikof Strait eggs, a comparison of developmental rates of walleye pollock eggs from the Bering Sea and Shelikof Strait at cold temperatures must be made. Bering Sea walleye pollock eggs are larger than those from Shelikof Strait (mean = 1.45-1.72 mm and 1.32-1.47 mm, respectively)(Kendall, 2001; AFSC unpubl.[2]) and the difference in size may affect development rates (Pepin, 1991; Pauly and Pullin, 1988). The degree of any differences between Bering Sea and Shelikof Strait walleye pollock egg incubation rates should be ascertained before incorporating the combined incubation data into one model.

The objective of this study was to incubate Bering Sea and Shelikof Strait walleye pollock eggs at low water temperatures such as those recorded in the Bering Sea in 1995 to document and compare development rates and determine whether eggs would develop normally. One group of Bering Sea eggs was exposed to a diel light cycle to determine what effect light would have on incubation. Egg development times were used to produce regression models for both Bering Sea and Shelikof Strait eggs to estimate egg age based on water temperature and developmental stage. The observed data and regression models were then compared to ascertain whether the cold-water data could be incorporated into an existing model for Shelikof Strait

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walleye pollock, based on warmer temperatures, to allow for a wider range of temperatures over which development rates can be modeled for both the Bering Sea and Shelikof Strait populations.

Methods

Adult walleye pollock were collected with a midwater trawl northwest of Unimak Island, Alaska (54°48.42'N, 165°26.39'W) in the Bering Sea near the 200 m isobath on 2 April 1997 from the NOAA ship *Miller Freeman*. Incubation methods follow Blood *et al.* (1994). Eggs from three females and milt from nine males were hand stripped, mixed together, and left undisturbed for about 5 min. Eggs were rinsed and transferred to 3°C seawater (ambient temperature) in glass jars (3.8 L). Eggs were held at 3°C for 2 h to determine viability (Blaxter, 1969; Alderdice, 1988), after which time many dead eggs had fallen to the bottom of the jars. Eggs that were floating were not counted but estimated at about 0.75/ml and poured into 30 1-L jars filled with 3°C seawater. Six capped jars were held in each of five water bath incubators onboard the *Miller Freeman*. Initial incubation temperatures were set at -1°, 0°, 2°, and 4°C. The lowest temperature was set no lower than -1°C because Nakatani and Maeda (1984) had reported high egg mortality and embryo malformations for walleye pollock eggs that had been reared at -1°C. The highest water temperature (4°C) was chosen to overlap the lowest incubation temperature of the previous model of Shelikof Strait walleye pollock eggs (Blood *et al.*, 1994). All but one of the incubators were sealed to minimize light and movement and placed in refrigerators. The fifth incubator was placed in the 4°C refrigerator near a fluorescent light; jars were not capped but covered by a thin nylon gauze secured by rubber bands to admit light and prevent the eggs from spilling out if the jars shifted. Light exposure was on a diel cycle (14 h light, 10 h dark) at a level inside the jars of approximately 45 &molßm^{-2}ßs^{-1}. This level is close to average levels typically found within the upper 20 m of the water column by Kendall *et al.* (1994) around Kodiak Island, Alaska in early May; expected light levels at the time the eggs were obtained and during the subsequent incubation period (April 2-23) would be lower. Eggs

were exposed to higher light levels than expected in the field to determine whether light would have any detrimental effect on development or incubation duration. One-half of the water in the jars was replaced every day with seawater of the same temperature.

Eggs were sampled every 2 h for the first 24 h, then every 4 h until the blastodermal cap developed (stage 7 - Blood *et al*., 1994), and every 8 h thereafter. At each sampling interval, 7-10 eggs were sampled from one jar per incubator; only one jar was sampled to leave enough eggs to last through the incubation and hatching period. Eggs were assigned a stage according to the 21-stage scheme described by Blood *et al*. (1994) and preserved in formalin (5%) buffered with sodium borate. Jars were sampled in rotation throughout the experiment until no eggs remained. Dead eggs were removed from the designated sample jar and water bath temperatures were recorded at each interval. When eggs began to hatch, all jars were checked and newly hatched larvae were removed and measured to the nearest 0.1 mm SL. The percentage of larvae measured during the hatching period at each treatment varied from 85% to 94%, depending on their condition and the number hatching at each sampling period. Average water temperatures in the darkened incubators were -0.6°, 0.4°, 2.0°, and 3.8°C; the average temperature in the incubator exposed to the diel light cycle was 3.9°C.

Shelikof Strait walleye pollock eggs were obtained from three female and six male fish collected 7 April 1998 southeast of Takli Island (57°59.83'N, 154°23.31'W) near the 200 m isobath. Onboard the *Miller Freeman*, eggs were handled as described for the Bering Sea experiment except they were apportioned into 18-1L jars at an estimated concentration of 1 egg/ml because there were fewer dead eggs at the end of the initial holding period. Jars were divided among three water bath incubators. All eggs were reared under dark conditions in refrigerators with initial incubation temperatures set at 0°, 2°, and 3°C. Actual temperatures in the incubators averaged 0.2°, 1.8°, and 2.8°C. The percentage of larvae measured was between 10% and 69% of the total number hatching.

Midpoint of stage was estimated for eggs incubated at each temperature within each group as described by Blood *et al*. (1994). Midpoints and time to 50% hatch were used to derive

piece-wise least-squares linear regression models (SAS, 1990) to estimate age (hours) of eggs at a specific stage incubated at any temperature within the limits of each experiment. Midpoints of stages were compared within temperatures between experiments and other studies using paired t-tests with pairs defined by egg stages.

Results

Bering Sea

Egg mortalities were high for the first 1-2 weeks. At all temperatures mortalities peaked at 16-20 h post fertilization; percent mortalities after the peak were inversely related to temperature except for the eggs exposed to diel light. Percentages of dead eggs varied from 36% (3.8°C) to 65% (0.4°C) (Table 1). Higher than expected percent egg mortalities for the 0.4° and 3.9°C (diel) groups were the result of greater initial numbers of egg deaths. The number of eggs sampled was reduced to an average of five per jar at each sampling period for the –0.6°C treatment in an effort to leave enough eggs to adequately document development. However, not enough eggs remained at –0.6°C to obtain hatch data to determine the midpoint of stage 21; therefore, only stages 1-20 were used for the regression model at that temperature.

Development of embryos was normal for all temperatures except –0.6°C, at which temperature some embryos were malformed. Gross abnormalities included tail malformations and the absence of eyes. Development rate of eggs incubated at 3.9°C under diel light was similar to that of eggs incubated at 3.8°C in constant dark prior to hatch (Table 2, Fig. 1). The pattern of hatch was similar for all eggs incubated under constant dark conditions; 50% of the larvae hatched approximately midway through the time required for all larvae to hatch. However, hatching of larvae from eggs incubated under diel light was delayed with 50% of the larvae hatching after 90% of the hatching period had elapsed. Hatching period (number of hours from first to last larva to hatch) decreased as incubation temperature increased for 0.4°, 2.0°, and 3.8°C treatments, but was greater for the 3.9°C diel treatment than it was for eggs incubated at 3.8°C in darkness. For eggs incubated under dark conditions, mean length of larvae at hatch

varied with no pattern in respect to temperature. Mean length of larvae at hatch for eggs incubated under the diel light cycle was greater than those incubated at a similar temperature in darkness (Table 1).

The piece-wise regression model (SAS,1990)(Fig.1) is similar to that in Blood *et al.* (1994): composed of two separate components and discontinuous between stages 6 (32+ cells) and 7 (blastodermal cap)(Fig. 2) because of the rapid divergence of developmental rates at all temperatures after stage 6. The two components are described by the following equations:

Component 1: stages 1-6

$$\text{Age} = -10.6 + 19.167(\text{stage}) - 0.364(\text{stage})(\text{temperature}) - 5.129(\text{stage}^2) + 0.588(\text{stage}^3) - 0.011(\text{stage}^3)(\text{temperature});$$

Component 2: stages 7-21

$$\text{Age} = -357.319 + 104.993(\text{stage}) - 6.946(\text{stage}^2) - 0.306(\text{stage}^2)(\text{temperature}) + 0.233(\text{stage}^3),$$

where age of the egg is expressed in hours. The value of R^2 is 0.98 for Component 1 and 0.97 for Component 2.

Shelikof Strait

Egg mortalities at 1.8° and 2.8°C peaked at 20 h post fertilization; percent mortalities were similar for both treatments for total incubation time (20%) and after the initial peak (15% and 14%, respectively)(Table 1). The percent mortality at these temperatures was similar to that observed in other incubation studies of walleye pollock eggs (Olla and Davis, 1993; Nakatani and Maeda, 1984). Egg deaths were greater for the 0.2°C eggs, which had a protracted period of high mortalities (69 h) and a higher percent mortality after the "peak" (39%) than the warmer treatments. The high percentage of dead eggs at 0.2°C, in comparison to the other treatments, indicates the temperature was below a tolerable threshold. Enough eggs survived at all temperatures to fully document development and 50% hatch.

Development was normal at all three temperatures but pattern of hatch varied among the three treatments. Midpoint of hatch occurred after 70% of the hatching period had elapsed at

0.2°C and after only 23% of the hatching period had elapsed at 1.8°C. Midpoint of hatch for eggs incubated at 2.8°C occurred about midway through the hatching period. Length of the hatching period at 1.8°C was longer than for either of the other two treatments. However, fewer than 1% of the eggs extended this period by 120 h. Mean length of larvae at hatch increased with temperature (Table 1).

The piece-wise regression model for the Shelikof Strait eggs (Fig. 1) is similar in format to the Bering Sea model and is described by the following equations:

Component 1: stages 1-6

$$\text{Age} = -10.6 + 17.643(\text{stage}) - 0.061(\text{stage})(\text{temperature}) - 5.382(\text{stage}^2) + 0.662(\text{stage}^3) - 0.028(\text{stage}^3)(\text{temperature});$$

Component 2: stages 7-21

$$\text{Age} = -52.288 + 27.669(\text{stage}) - 1.099(\text{stage}^2) - 0.412(\text{stage}^2)(\text{temperature}) + 0.1(\text{stage}^3).$$

The value of R^2 for both components is 0.98.

Development rates of both Bering Sea and Shelikof Strait walleye pollock eggs were compared to those of other studies at or near 0°, 2°, and 4°C (Fig. 3). Using a paired t-test with the pairs defined by egg stages, a significant difference ($P<0.05$) was found between comparable estimated midpoints (h) of five stages reported by Haynes and Ignell (1983) and observed stage midpoints of both Bering Sea and Shelikof Strait eggs at 2°C. There was also a significant difference ($P<0.05$) between observed stage midpoints from Blood *et al.* (1994) and the Bering Sea eggs at 3.8°C.

Discussion

Morphological development at all temperatures >0°C was normal. Only those embryos incubated at –0.6°C had misshapen tails, similar to what Nakatani and Maeda (1984) had reported in eggs reared at –1°C, or had not developed eyes. Walleye pollock eggs developing in areas with temperatures <0°C would experience higher mortality rates due to growth abnormalities and may be at greater risk of predation because of the increased length of

incubation. The degree to which growth abnormalities would affect mortality cannot be determined from this study.

When development rates of Bering Sea and Shelikof Strait walleye pollock eggs were compared to those of other studies at similar temperatures (Fig. 3), results at colder temperatures were different than expected. Shelikof Strait walleye pollock eggs required more time to reach midpoints of four developmental milestones and 50% hatch than times estimated for Haynes and Ignell (1993) at temperatures at or about 2°C. Although Haynes and Ignell (1993) did not report egg diameters, it is assumed that their size was similar to that of the Shelikof Strait eggs (Bailey and Stehr, 1986). Therefore, egg development times were expected to be similar for both studies. Blood *et al.* (1994) compared time to 50% hatch between eastern and western North Pacific walleye pollock incubation studies at 2-11°C and found that at all temperatures western North Pacific walleye pollock required more time to reach 50% hatch than eastern North Pacific walleye pollock. Although a comparison of four midpoints of stages prior to hatch of Bering Sea or Shelikof Strait eggs with a western North Pacific incubation study that encompassed the same low temperatures as this study (Nakatani and Maeda, 1984) was not statistically significant at any temperature, at temperatures close to 0°C both Bering Sea and Shelikof Strait walleye pollock eggs required more time (26 and 250 h, respectively) to reach 50% hatch. At temperatures close to 2°C, Bering Sea eggs required less time (25 h) and Shelikof Strait eggs reached 50% hatch at a similar time as Nakatani and Maeda (1984). Bering Sea eggs required 51 h less than Nakatani and Maeda (1984) to reach 50% hatch at temperatures close to 4°C. Walleye pollock eggs from Japanese waters are similar in size to those in the Bering Sea (mean = 1.4-1.6 and 1.45-1.72, respectively)(Bailey and Stehr, 1986; Kendall, 2001) and larger than those from Shelikof Strait (mean = 1.32-1.47 mm) (AFSC unpubl.[2]). In these comparisons, egg size appears to have less influence on time to 50% hatch at temperatures $\leq$2°C than at higher temperatures.

The difference in hatching pattern between the eggs incubated at 3.9°C under diel light and those incubated at 3.8°C in constant dark was similar to that described by Olla and Davis

(1993) for eggs from Shelikof Strait, although the delay of 50% hatch for this study was more extreme (their 50% hatch for the diel group occurred after 75% of the hatching period had elapsed) (Table 1). Intensity of light during incubation was greater during this study (45 &molßm^{-2}ßs^{-1}) than for Olla and Davis (1993)(28 &molßm^{-2}ßs^{-1}); it is not known if the difference in time of 50% hatch is the result of the difference in light intensity or if walleye pollock eggs from the Bering Sea and Shelikof Strait differ in their response to light.

Overall mean length of larvae at hatch was 14% greater for eggs incubated under diel light than those kept in constant dark. Difference in incubation temperatures between the two treatments would have a negligible impact on the disparity in lengths: Blood *et al*. (1994) reported an increase in mean length of newly hatched larvae of only 0.4 mm SL over a temperature span of 3.9°C and in this study there was an increase of 0.4 mm SL over both temperature spans of 3.4°C (Bering Sea) and 2.6°C (Shelikof Strait). At 424 h post-fertilization, which is the time of 50% hatch of larvae from eggs incubated under dark conditions, mean length of larvae at hatch in the diel treatment was approximately the same as those in constant dark (~4.9 mm SL, Fig. 4). The difference in mean length at 50% hatch of 0.7 mm SL is the result of an additional 72 h of incubation at an advanced stage of development. Exposure to similar levels of light as used in this study resulting in increased length at hatch may be favorable for larvae because it may reduce predation rates (Miller *et al*., 1988) and increase feeding success. It is not known if this advantage would outweigh the increased risk of predation that may result from the delay in hatching or the potentially shorter first feeding stage resulting from lower yolk reserves. Although exposure to the ultraviolet B component of solar radiation induces mortality in fish eggs, only the eggs in the upper meter of the water column would be adversely affected (Béland *et al*., 1999). Large numbers of walleye pollock eggs in the Bering Sea have been collected in the neuston (0.25 m)(Waldron and Vinter, 1978), but their mean depth over the shelf is about 25 m (Kendall, 2001).

Comparison of beginning of hatch, stage of development at that time, and midpoint of hatch (50% hatch) of the Bering Sea and Shelikof Strait eggs revealed differences between the

two groups. These parameters were compared for two similar temperatures: 0.4 and 2.0°C treatments for Bering Sea eggs and 0.2 and 1.8°C treatments for Shelikof Strait eggs (Fig. 5). For both comparisons, beginning of hatch occurred earlier for the Bering Sea larvae; 96 h earlier than the Shelikof Strait group for temperatures close to 0°C and 80 h earlier for temperatures close to 2°C. Whereas there are direct relationships between increasing temperature and beginning of hatch, a difference of 0.2°C between the Bering Sea and Shelikof Strait groups does not appear to be the sole reason for the disparity. Difference in the onset of hatch between the 3.8 and 3.9°C treatments of Bering Sea larvae for this study was only 8 h; Blood *et al*. (1994) reported a difference of 63 and 77 h for onset of hatch between groups incubated at temperatures that were 2.0 and 2.1°C apart, respectively. The stage of development of the embryos at the beginning of hatch for this study also reflected the difference between the two groups: Bering Sea larvae began to hatch 36-44 h before the midpoint of stage 20, whereas the Shelikof Strait larvae were 6-39 h past the midpoint of stage 20. Midpoint of hatch also occurred earlier (in absolute hours) for the Bering Sea larvae, but a more meaningful comparison between the two groups is the percent of the hatching period that has elapsed at the point of 50% hatch. This point occurred after 35 and 56% of the hatching period had passed for the Bering Sea larvae at 0.4° and 2.0°C, respectively, and after 70 and 23% of the hatching period for the Shelikof Strait larvae at 0.2° and 1.8°C, respectively. The differences in hatching patterns of the two groups suggests that the Bering Sea eggs respond more consistently to the lower temperatures than the Shelikof Strait eggs. When hatching began for Shelikof Strait eggs, those reared at 0.2°C were developmentally less mature than eggs reared at 1.8°C and required more than twice the number of hours (224 h versus 86 h) to reach 50% hatch despite having a shorter hatching period (Table 1).

Although the regression equations in this study were similar in format for the Bering Sea and Shelikof Strait groups, three of the five parameters within the components predicting stages 7-21 (Component 2) were significantly different ($P<0.05$). When predicted time to reach the midpoint of stages 7-21 was compared between models, Bering Sea eggs consistently required

more incubation time than Shelikof Strait eggs at 1.8° and 2.8°C (Fig. 6). A similar comparison at 0.2°C was inconclusive. The regression equations to estimate egg age are different from the equations developed by Blood *et al.* (1994); Component 1 incorporates a cubic term within five parameters as opposed to their three parameters with a squared term and Component 2 has a squared interaction term as opposed to their cubic interaction term. Although a comparison of predicted time to reach midpoints of stages cannot be made between Bering Sea eggs in this study and Blood *et al*. (1994) because of these differences in regression equations, we can compare data because eggs were incubated at 3.8°C in both studies (Fig. 7). Times to reach midpoints of stages for the Bering Sea eggs were significantly greater ($P<0.05$) than for Shelikof Strait eggs from Blood *et al*. (1994). The difference in time needed to reach similar stages of development demonstrates that Bering sea walleye pollock eggs are slower to develop than Shelikof Strait eggs at 1.8 - 3 .8°C. Bering Sea walleye pollock eggs (mean = 1.45-1.72 mm) are larger than those from Shelikof Strait (mean = 1.32-1.47 mm)(Kendall, 2001; AFSC, unpubl.[2]). At similar incubation temperatures, larger eggs generally take longer to develop (Pepin, 1991; Pauly and Pullin, 1988). Since the Bering Sea eggs required more time to develop it is not possible to combine these data with the warmer temperature data for Shelikof Strait eggs generated by Blood *et al*. (1994) to produce a model of temperature specific development rates for walleye pollock eggs over the range of temperatures used in these studies (–0.6 - 7 .7°C). The low temperature regression model generated for Shelikof Strait eggs in this study can be used in conjunction with the model from Blood *et al*. (1994), but the data cannot be combined with the warmer temperature data to produce one model covering a wider range of temperatures because there is a gap in data between 2.8° and 3.8°C.

Interannual variability of the ecosystem in the Bering Sea, specifically dramatically low ocean temperatures, could affect walleye pollock egg survival. Unlike walleye pollock eggs in Shelikof Strait, which reside at depths of 150-200 m that vary little in temperature, Bering Sea shelf walleye pollock eggs are distributed throughout the water column which is <100 m deep and subject to substantial temperature variations. Ocean temperatures at a moored platform

(Mooring 2; 56.9°N, 164°W), integrated at 11-55 m, varied from –1.5 to 2°C between 1995 and 1998 during the time period when walleye pollock eggs would be present (Fig.8) (Stabeno *et al*., In press). When 50% hatch dates were estimated using the regression model for average temperatures for each year, the incubation period varied as much as 13 days between the coldest year (1997)[3] and the warmest (1998). Extending the incubation period by 13 days may subject walleye pollock eggs to greater possibility of predation and increased risk of malformations from exposure to extreme low temperatures. Although walleye pollock eggs are found throughout the water column, many are found within the upper 20 m and may be exposed to temperatures colder than those mentioned previously (Kendall, 2001). It is not known what the low temperature tolerances are for walleye pollock eggs for short periods of time.

[3] Egg development times for –0.6%C were used for ocean temperatures Æ–0.6%C, therefore the estimated 50% hatch date for 1997 may be later than indicated.

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List of Tables

Table 1

Low temperature egg incubation and hatch data for Bering Sea and Shelikof Strait walleye pollock (***Theragra chalcogramma***).

	Treatments (° C)	Length of incubation (h)*	Total % Egg mortality	% Egg mortality after peak	Time to 50% hatch (h)*	Length of hatching period (h)*	% Hatching period elapsed at time of 50% hatch	Overall mean length of larvae at hatch (mm SL)
Bering Sea								
	-0.6	1124	52	35	-----	-----	-----	-----
	0.4	1012	65	28	820	272	35	4.6
	2.0	844	45	28	620	256	56	5.2
	3.8	500	36	21	424	144	55	5.0
	3.9 (diel)	516	48	23	496	152	90	5.7
Shelikof Strait								
	0.2	1157	53	39	1044	321	70	4.2
	1.8	932	20	15	644	376	23	4.3
	2.8	716	20	14	526	240	44	4.6

* hours

Table 2

Midpoint in hours (h) of stage of development of Bering Sea and Shelikof Strait walleye pollock (***Theragra chalcogramma***) eggs incubated at low temperatures.

	Bering Sea					Shelikof Strait		
Stage [1]	-0.6°C (h)	0.4°C (h)	2.0°C (h)	3.8°C (h)	3.9°C (diel) (h)	0.2°C (h)	1.8°C (h)	2.8°C (h)
1	5	4	3	3	3	2.5	2.5	2.5
2	12	11	9	8	8	7.5	7	6.5
3	18	16	13	12	12	12.5	10.5	9
4	27	20	16	15	15	17	14	11.5
5	34	25	21	18	18	22.5	19	14.5
6	51	46	35	30	30	42.5	38	24.5
7	120	94	75	60	60	105.5	81.5	56.5
8	203	147	114	84	84	168	120.5	91
9	248	182	135	100	98	210	140	107.25
10	274	205	156	116	116	246	156	122.25
11	304	232	172	129	129	270	174	142
12	368	278	199	142	140	308	196	162
13	420	322	224	154	152	348	214	176
14	440	348	233	168	168	400	226	190
15	508	394	261	193	193	456	266	208
16	580	444	304	216	214	492	316	224
17	616	474	334	236	234	532	344	248
18	768	538	404	290	282	616	396	292
19	936	652	474	342	336	730	464	352
20	996	768	512	368	368	814	517	428
21	-----	820 [2]	620 [2]	424 [2]	496 [2]	1044 [2]	644 [2]	526 [2]

[1] See Blood ***et al***. 1994.
[2] 50% hatch.

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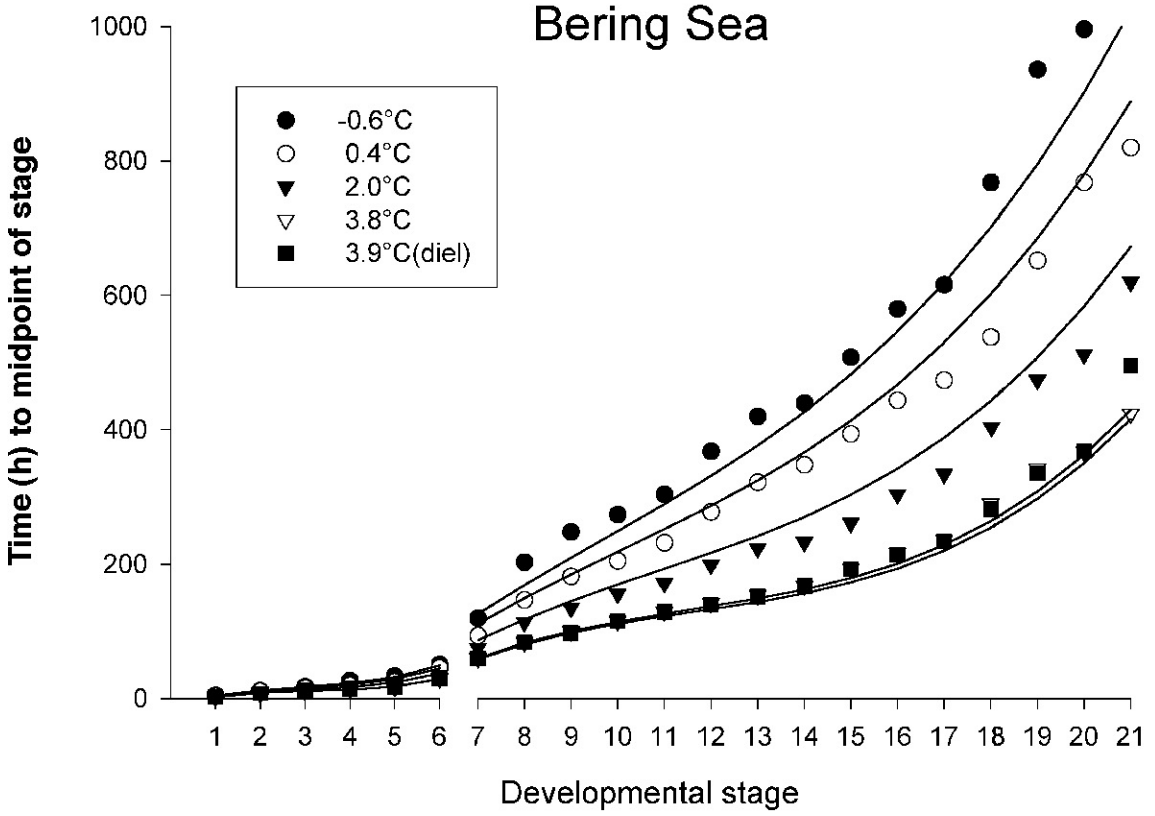
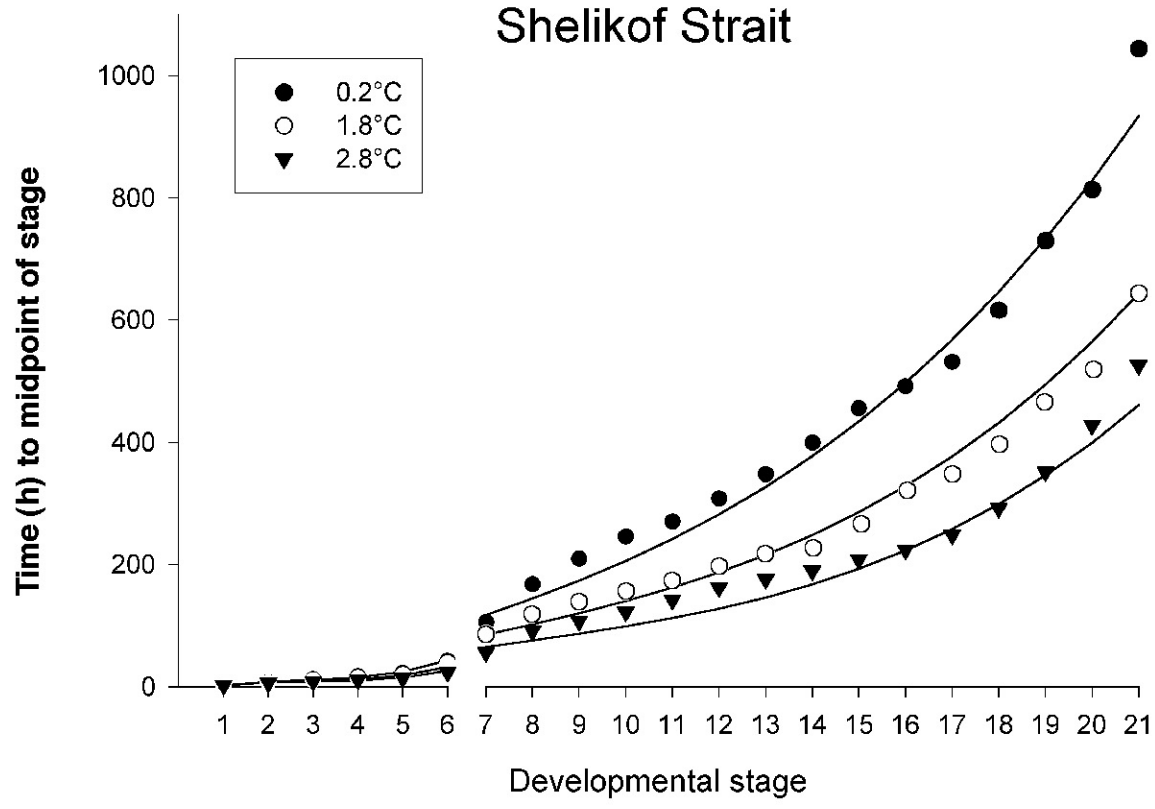
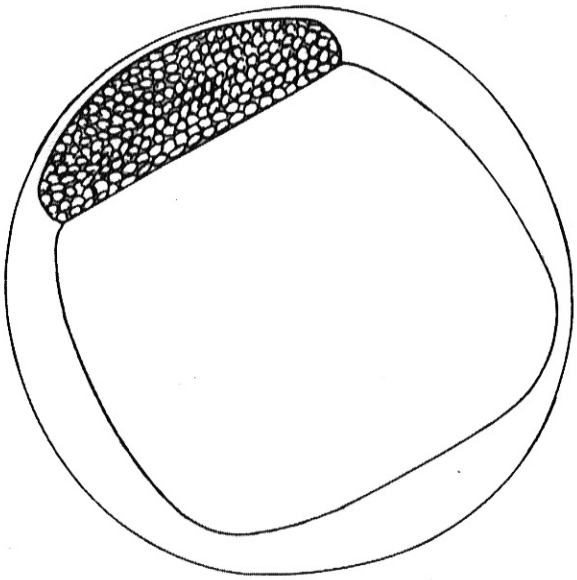
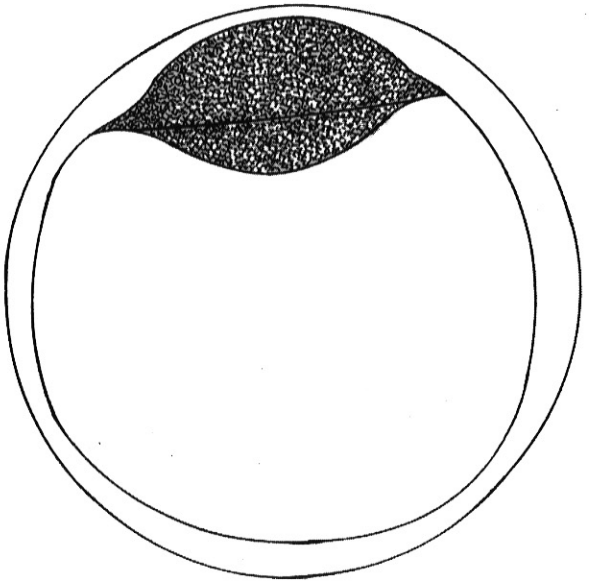

Bering Sea
-0.6°C
0.4°C
2.0°C
3.8°C
3.9°C(diel)
Time (h) to midpoint of stage
Developmental stage
0
200
400
600
800
1000
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21


Shelikof Strait
0.2°C
1.8°C
2.8°C
Time (h) to midpoint of stage
Developmental stage
0
200
400
600
800
1000
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21

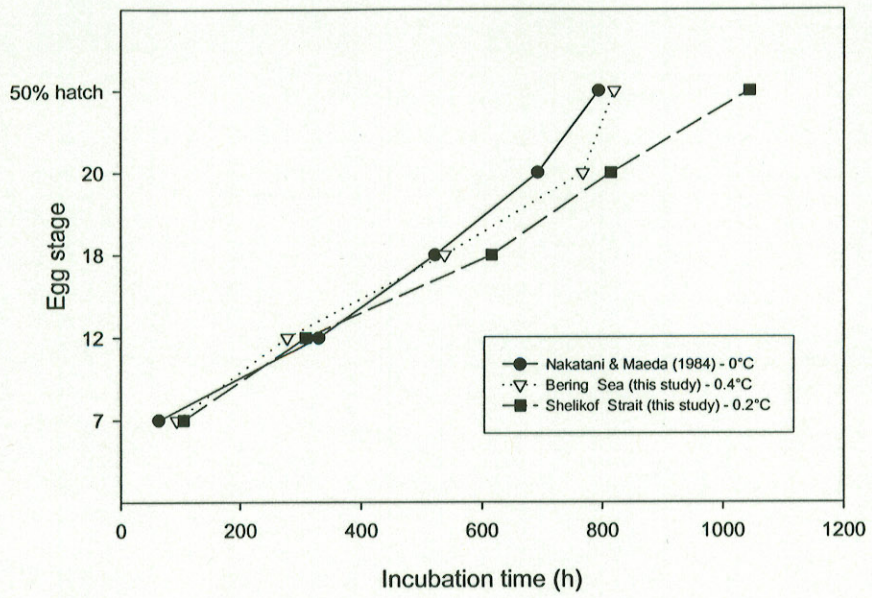


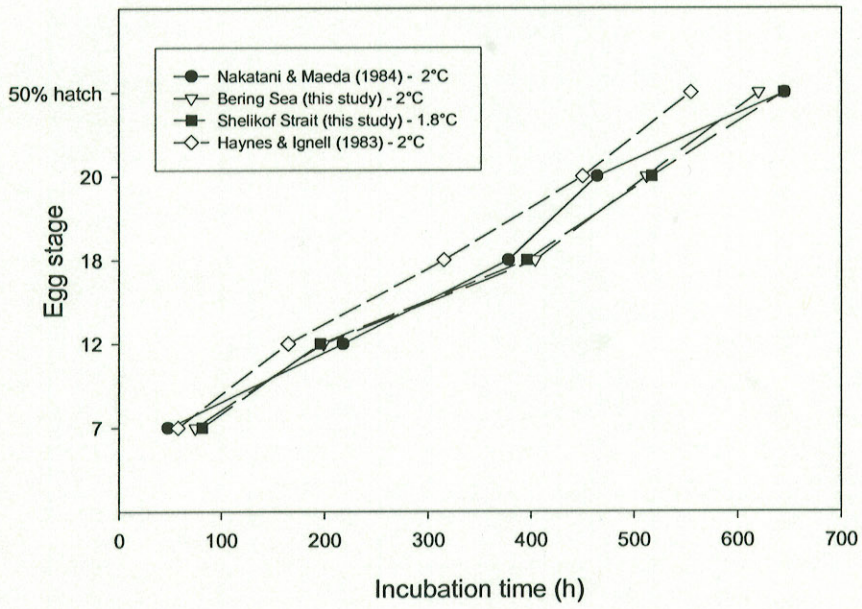
Stage 6



Stage 7

Figure 2


50% hatch
20
18
12
7
Egg stage
0
200
400
600
800
1000
1200
Incubation time (h)
Nakatani & Maeda (1984) - 0°C
Bering Sea (this study) - 0.4°C
Shelikof Strait (this study) - 0.2°C


50% hatch
20
18
12
7
Egg stage
0
100
200
300
400
500
600
700
Incubation time (h)
Nakatani & Maeda (1984) - 2°C
Bering Sea (this study) - 2°C
Shelikof Strait (this study) - 1.8°C
Haynes & Ignell (1983) - 2°C

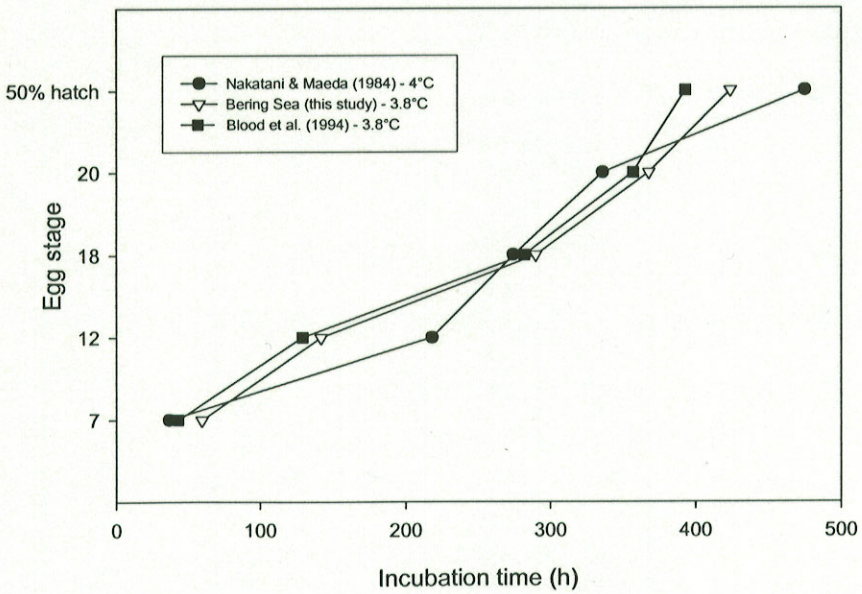
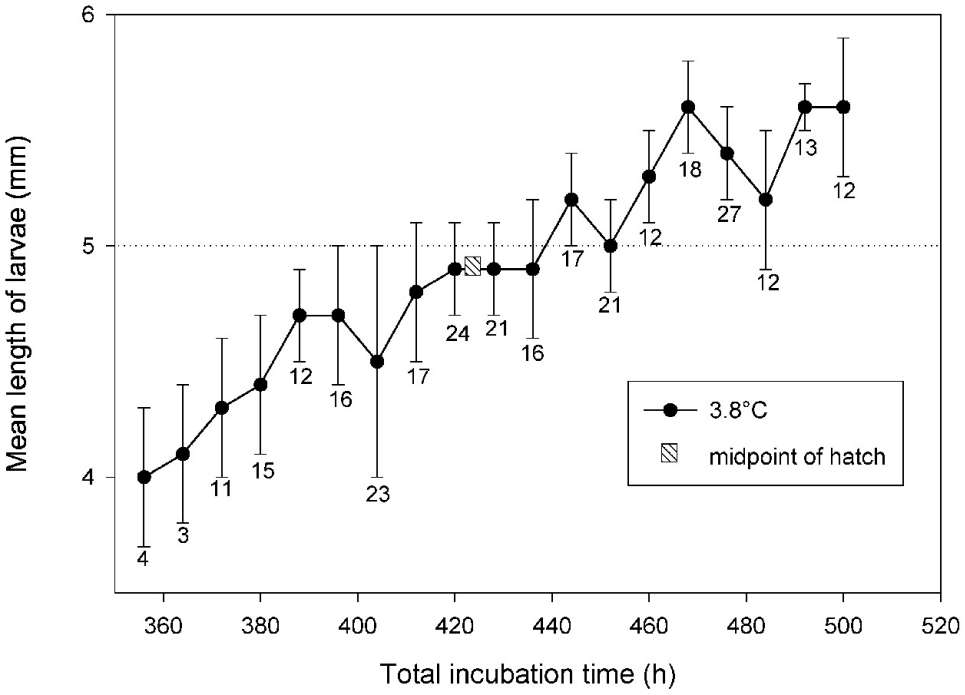
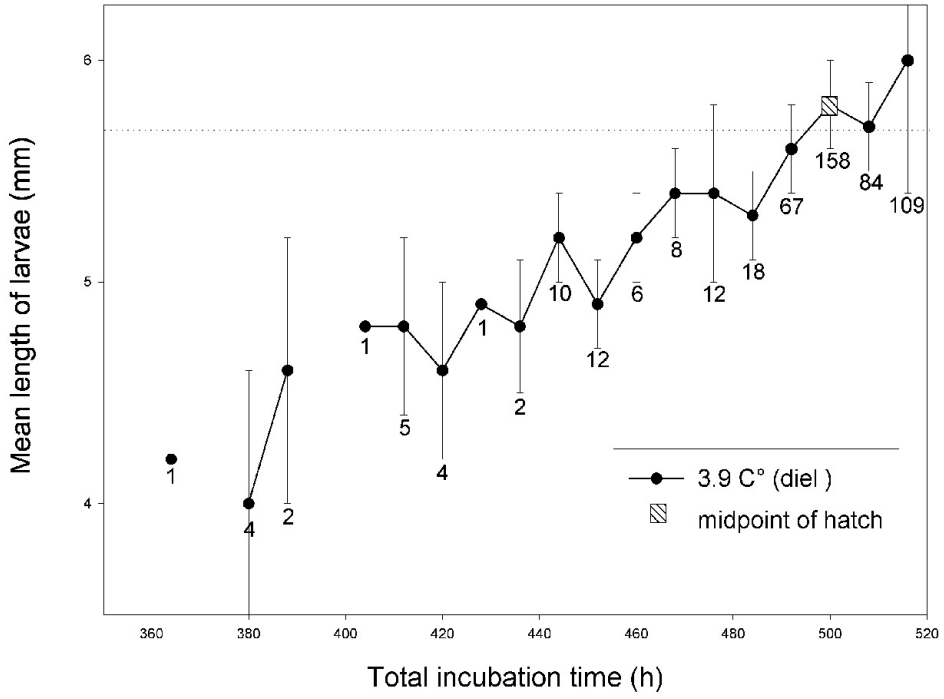
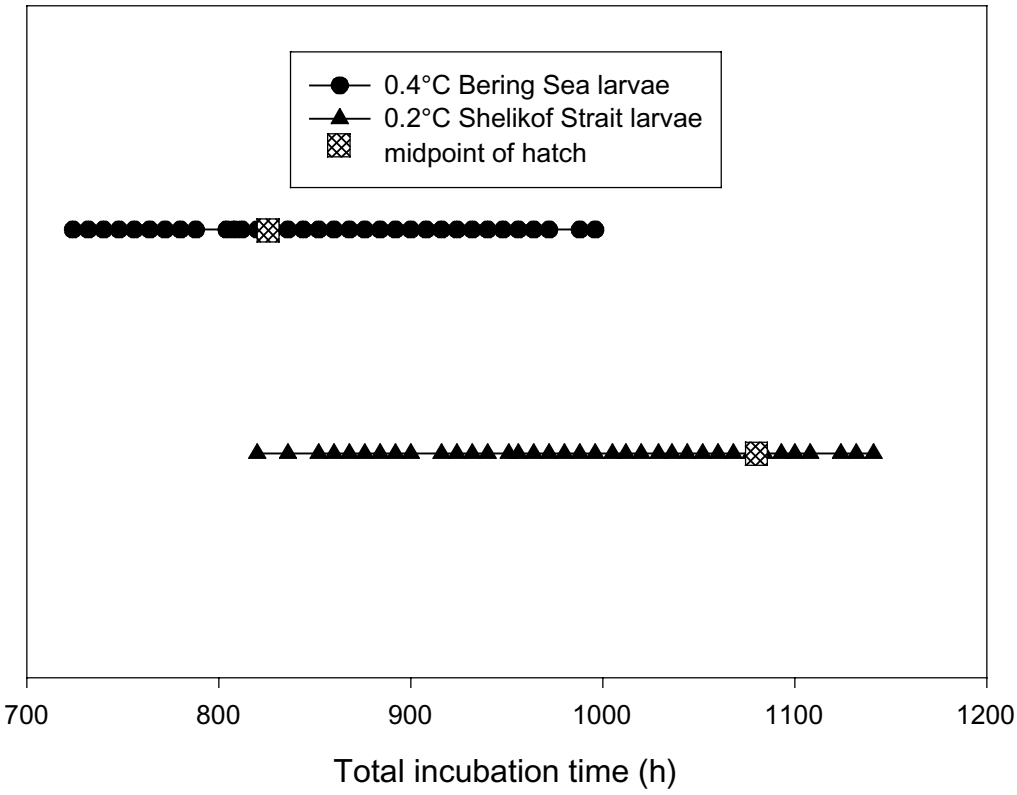

50% hatch
20
18
12
7
Egg stage
0
100
200
300
400
500
Incubation time (h)
Nakatani & Maeda (1984) - 4°C
Bering Sea (this study) - 3.8°C
Blood et al. (1994) - 3.8°C

Figure 3


Mean length of larvae (mm)
6
5
4
360
380
400
420
440
460
480
500
520
Total incubation time (h)
4
3
11
15
12
16
23
17
24
21
16
17
21
12
18
27
12
13
12
3.8°C
midpoint of hatch


Mean length of larvae (mm)
6
5
4
360
380
400
420
440
460
480
500
520
Total incubation time (h)
1
4
2
1
5
4
1
2
10
12
6
8
12
18
67
158
84
109
3.9 C° (diel)
midpoint of hatch


0.4°C Bering Sea larvae
0.2°C Shelikof Strait larvae
midpoint of hatch
700
800
900
1000
1100
1200
Total incubation time (h)

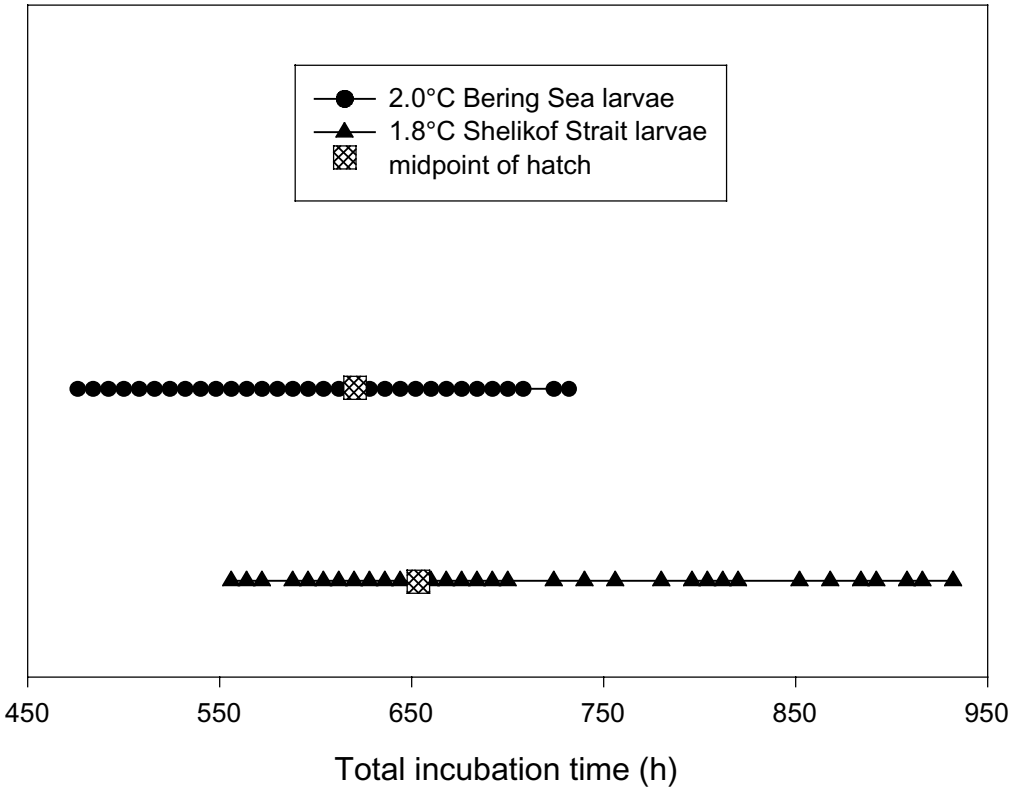

2.0°C Bering Sea larvae
1.8°C Shelikof Strait larvae
midpoint of hatch
450
550
650
750
850
950
Total incubation time (h)

Figure 5

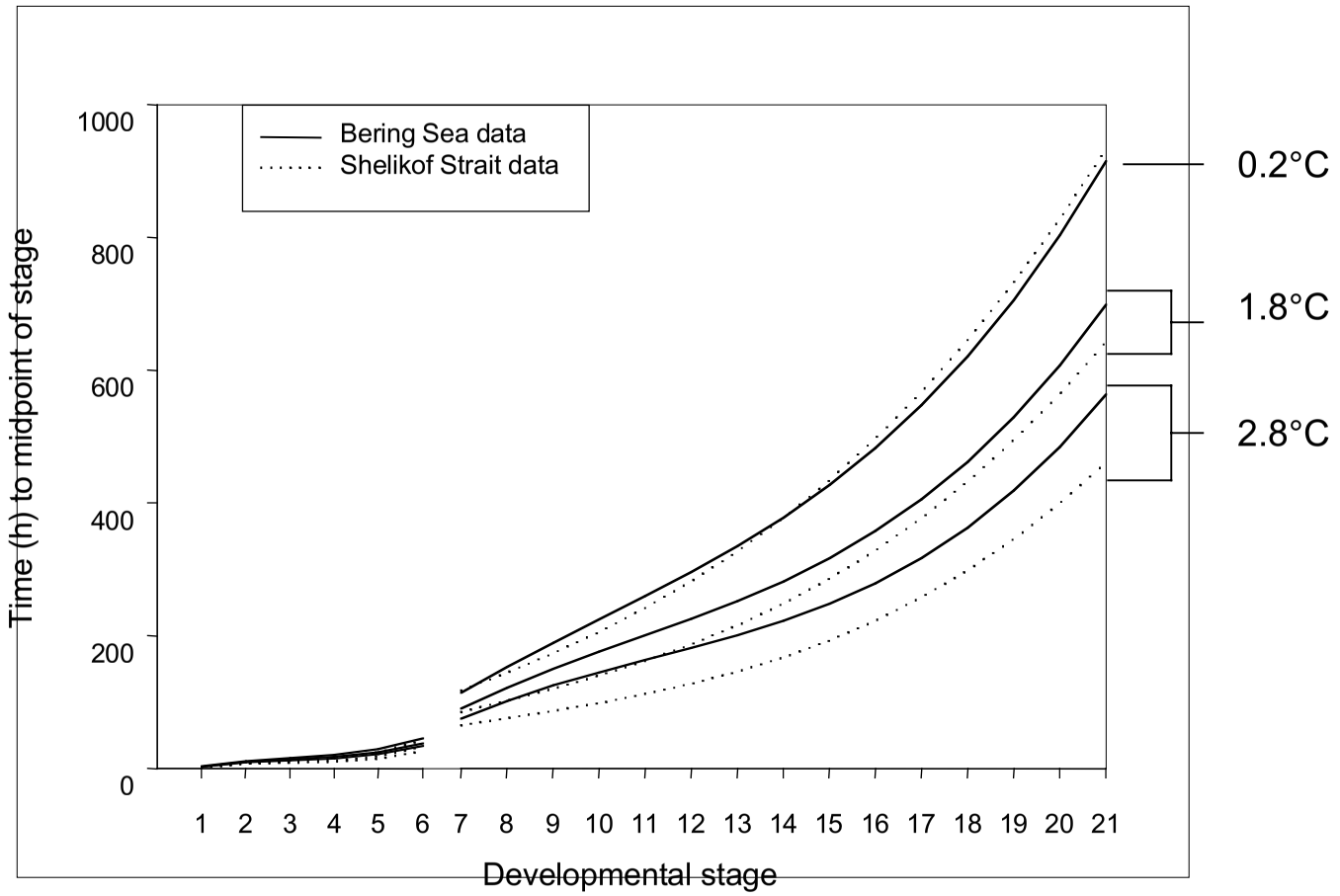

Bering Sea data
Shelikof Strait data
Time (h) to midpoint of stage
1000
800
600
400
200
0
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
Developmental stage
0.2°C
1.8°C
2.8°C

Figure 6

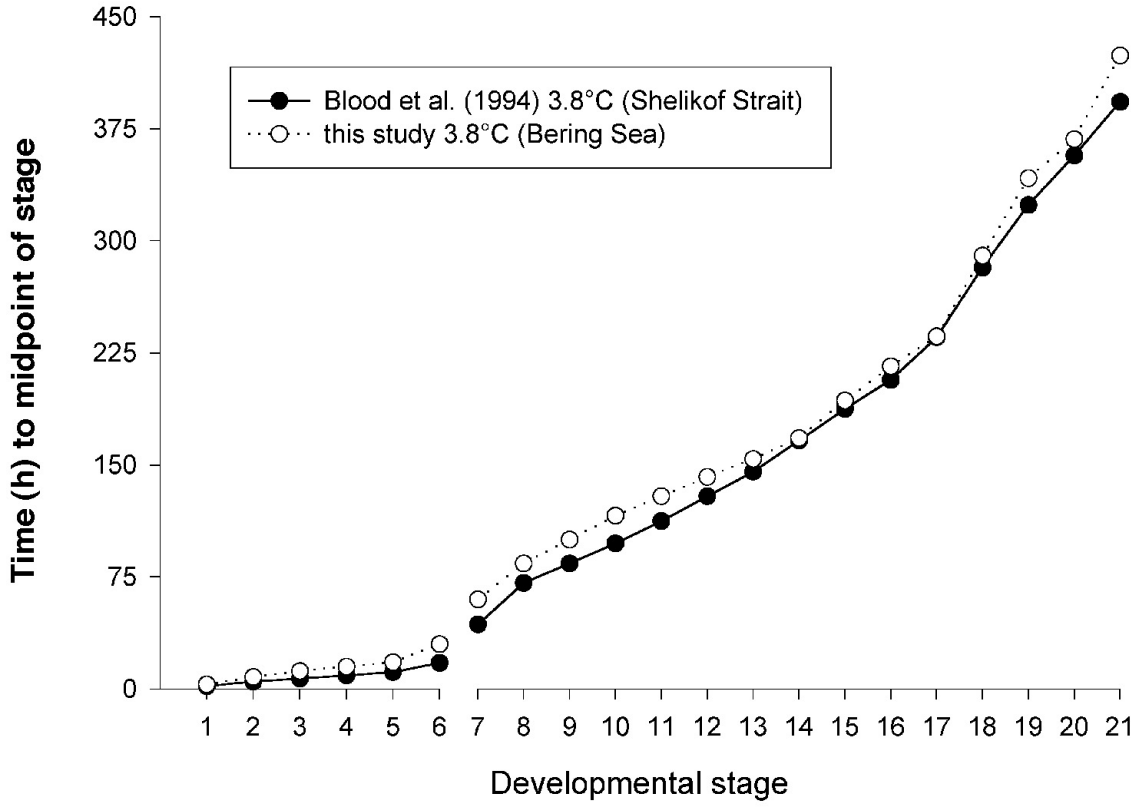

Blood et al. (1994) 3.8°C (Shelikof Strait)
this study 3.8°C (Bering Sea)
Time (h) to midpoint of stage
Developmental stage
0
75
150
225
300
375
450
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21

Figure 7

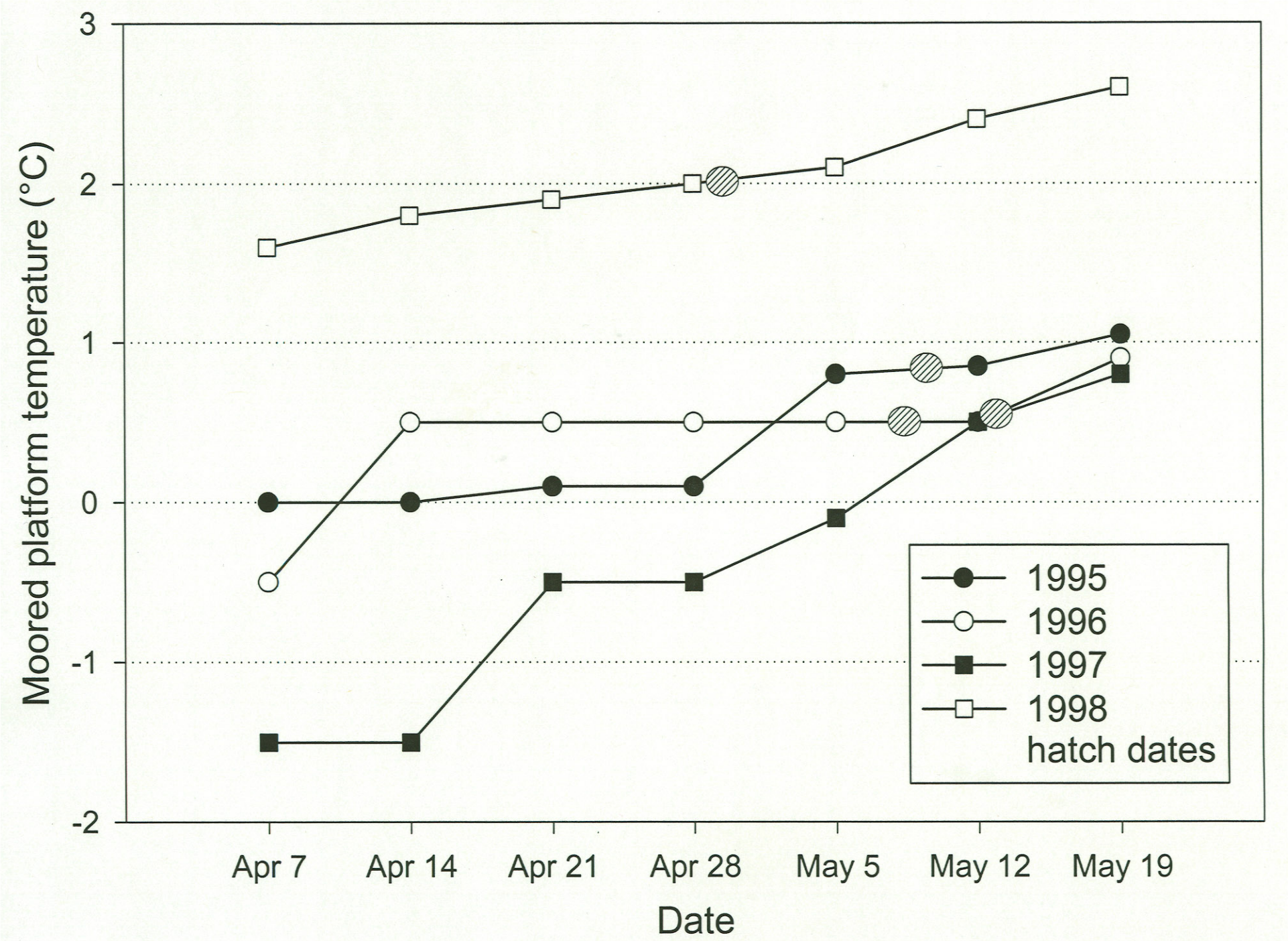

3
2
1
0
-1
-2
Moored platform temperature (°C)
Apr 7
Apr 14
Apr 21
Apr 28
May 5
May 12
May 19
Date
1995
1996
1997
1998
hatch dates

Figure 8